[Palaeontology, Vol. 52, Part 5, 2009, pp. 1099–1112]

A NEW ARTHROPOD RESTING TRACE AND ASSOCIATED SUITE OF TRACE FOSSILS FROM THE LOWER JURASSIC OF WARWICKSHIRE, ENGLAND

by LORNA J. O'BRIEN*†, SIMON J. BRADDY† *and* JONATHAN D. RADLEY‡

*Royal Ontario Museum, 100 Queen's Park, Toronto, ON M5S 2C6, Canada; e-mail lornao@rom.on.ca
†Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK
‡School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK

Typescript received 26 May 2008; accepted in revised form 25 November 2008

Abstract: A new suite of arthropod trace fossils, attributed to a decapod crustacean, is described from the Lower Jurassic Saltford Shale Member of the Blue Lias Formation of Southam Cement Works Quarry, eastern Warwickshire, England. *Solusichnium southamensis* igen. et isp. nov. consists of small, isolated, bilaterally symmetrical, suboval hypichnia, comprising three regions. The concave anterior region contains imprints of chelate appendages, antennae and antennules. The elongate middle region contains abdominal appendage imprints that extend laterally, separated by a bifurcated medial imprint. The convex posterior region terminates in a globular V-shaped telson imprint. The large sample size and range of trace morphologies allows identification of five morphotypes within a taphoseries. *S. southamensis* is found on the base of siltstone lenses in what is otherwise a dysaerobic laminated mudstone unit, associated with epichnial *Rusophycus*, and the suite of trace fossils is interpreted as the resting traces (Cubichnia) and escape reactions (Fugichnia) of small decapods that were trapped below a distal storm deposit. The producer of *S. southamensis* was possibly an *Eryon*-like decapod, similar to those known from the slightly older Wilmcote Limestone Member of southwestern Warwickshire.

Key words: ichnotaxonomy, Cubichnia, Fugichnia, *Solusichnium southamensis* igen. et isp. nov., *Rusophycus*, decapod, Blue Lias Formation.

THE study of trace fossils (ichnology) has undergone a revolution in recent years, and their potential for palaeoenvironmental reconstruction is becoming increasingly realised (e.g. McIlroy 2004). Trace fossils (ichnofossils) are often found in sediments that are devoid of body fossils and thus sometimes the only evidence for life in certain palaeoenvironmental settings. Trace fossils provide direct evidence for the behaviour and activities of organisms in a way that body fossils never can; they almost invariably occur *in situ* and may allow the stratigraphic ranges and environmental distribution of their producers to be improved. However, difficulties arise when trying to infer the producers of trace fossils, as many organisms may produce the same type of trace fossil (ichnotaxon) and one organism may produce a number of different ichnotaxa.

Because of their method of emplacement, resting traces (Cubichnia) are often likely to preserve details of the morphology of their producer, especially its ventral surface, which constrains interpretations of their potential producers (Table 1). Unless a body fossil is observed in direct association with a trace fossil (i.e. so-called Mortichnia of Seilacher 2007, p. 75), the identity of the trace maker is open to interpretation. However, associated body fossils have been used to convincingly indicate potential producers (e.g. Fortey and Seilacher 1997 on the producer of *Cruziana semiplicata*).

Arthropod-produced resting traces are well known from the fossil record (Table 1). The term 'resting trace' is often misinterpreted to simply imply a trace made by an animal as it passively settles into or on the sediment. These discrete traces, however, often result from various behaviours, including concealment, feeding, a temporary halt in locomotion (e.g. jumping) respiration or escape (e.g. Crimes 1975; Buatois *et al.* 1998; Braddy and Briggs 2002; Martin 2006; Seilacher 2007). This is demonstrated best by the range of ethological categories that have been suggested for different 'arthropod resting traces' (Table 1). The morphology of any trace fossil, including arthropod resting traces, is determined by the interaction between the producer's anatomy, its behaviour and substrate consistency (Minter *et al.* 2007*a*).

A suite of arthropod trace fossils is described from the Early Jurassic Saltford Shale Member of the Blue Lias Formation (Hettangian; Liasicus to Angulata Chronozone) from Southam Cement Works Quarry, eastern

 doi: 10.1111/j.1475-4983.2009.00901.x

TABLE 1. Known arthropod resting trace ichnogenera (excluding *Rusophycus*, which has more than 30 ichnospecies), including the known ichnospecies, age ranges, proposed ethology and proposed producers. This table excludes ichnogenera that are now considered invalid.

Ichnogenus/Ichnospecies (Author and year)	Age	Ethology	Producers
Aglaspidichnus sanctacrucensis (Radwanski and Roniewicz, 1967)	Cambrian	Cubichnia	Aglaspidida
Avolatichnium dipedum (Walter, 1983)	Permian	Volichnia	Insecta (adult)
Broomichnium permianum (Kuhn, 1958)	Permian	Cubichnia	Piscine
B. fliri (Benner *et al.*, 2008)	Pleistocene	Repichnia	Piscine
Chagrinichnites brooksi (Feldmann *et al.*, 1978)	Devonian	Cubichnia	Crustacea: Eocarida
C. osgoodi (Hannibal and Feldmann, 1983)	Devonian	Fugichnia	Crustacea: Phyllocarida
Gluckstadella cooperi (Savage, 1971)	Carboniferous Permian	Cubichnia	Arthropoda (unspecified)
Hedriumichnus apacheensis (Braddy and Briggs, 2002)	Permian	Cubichnia	Insecta: Ephemeroptera or Plecoptera
'Isopodichnus' furcosus (Gand, 1994)	Permian	Cubichnia	Crustacea: Notostraca
Ixalichnus enodius (Callison, 1970)	Cambrian	Cubichnia	Trilobita
Kingella natalensis (Savage, 1971)	Carboniferous Permian	Cubichnia	Crustacea: Syncarida or Peracarida
Limulicubichnus serratus (Miller, 1982)	Carboniferous	Cubichnia	Xiphosurida: Limulidae
Orbiculichnus vulgaris (Holub and Kozur, 1981)	Permian	Volichnia	Insecta: Pterygota
Pollichianum cubichnum (Heidtke, 1990)	Permian	Cubichnia	Crustacea: Astacidea
P. repichnum (Heidtke, 1990)	Permian	Repichnia	Crustacea: Astacidea
Pseudobilobites jefferiesi (Kennedy, 1967)	Cretaceous	Cubichnia	Crustacea: Cumacea
Raaschichnus gundersoni (Hesselbo, 1988)	Cambrian	Cubichnia	Aglaspidida
Rotterodichnium longinum (Walter, 1983)	Permian	Volichnia	Insecta: Protodonata, Odonata, or Megasecoptera
R. major (Braddy and Briggs, 2002)	Permian	Volichnia	
Selenichnites hundalensis (Romano and Whyte, 1987)	Jurassic	Cubichnia	Xiphosurida
S. rossendalensis (Hardy, 1970)	Carboniferous	Cubichnia	Euthycarcinida
S. cordiformis (Fischer, 1978)	Ordovician	Cubichnia	Crustacea
S. langridegi (Trewin and McNamara, 1995)	Ordovician	Cubichnia	Crustacea
S. antarcticus (Weber and Braddy, 2004)	Ordovician	Cubichnia	Crustacea
Svalbardichnus trilobus (Wisshak *et al.*, 2004)	Devonian	Cubichnia	Crustacea: Phyllocarida
Tripartichnus triassicus (Vallon and Röper, 2006)	Triassic	Cubichnia	Euthycarcinida
T. imbergi (Vallon and Röper, 2006)	Jurassic	Cubichnia	Crustacea: Palinuridae
Tonganoxichnus buildexensis (Mángano *et al.*, 1997)	Carboniferous	Cubichnia	Insecta: Monura
T. ottawensis (Mángano *et al.,* 1997)	Permian	Pascichnia	Insecta: Monura
T. robledoensis (Braddy and Briggs, 2002)	Permian	Repichnia	Insecta: Monura

Warwickshire, England. Over 150 specimens, representing a range of preservational variations, allow the identification of both morphological and taphonomic features within the fossils.

Much of the Saltford Shale at the Southam Quarry lacks any ichnofauna (Radley 2002, 2008): a sparse macrofauna dominated by ammonites, nautiloids, bivalves and rare ichthyosaur, plesiosaur and fish remains are known. The scarcity of benthic fauna reflects dysaerobic bottom water conditions (Radley 2002, 2008). The only crustacean known from the Saltford Shale Member is an undescribed, small, disarticulated isopod-like specimen. However, the slightly older Wilmcote Limestone Member (Rhaetian to Hettangian; Planorbis Chronozone) of southwestern Warwickshire has yielded many arthropod body fossils including three decapod species (Woodward 1893) that are demonstrated to be potential producers of these new trace fossils.

TRACE FOSSIL CLASSIFICATION

Preservation, morphological complexity, proposed producers, size, stratigraphic age, environment and expressed behaviour (ethology) have been used previously to classify trace fossils. Seilacher (2007, p. 92) argues that trace fossil names are inherently unstable through time because of differing interpretations and unrecognised synonymy, and that the current nomenclature is perhaps not the best way to classify trace fossils. The argument centres on nomenclature and classification being incompatible: the former is concerned only with attaching a label to a fossil for ref-

erence purposes, and the latter with inferring relationships between groups of trace fossils. Recent consensus regarding the naming of trace fossils (Bertling *et al.* 2006) has provided clarification for the valid naming of trace fossils.

Such systematic problems are exemplified by the ichnogenus *Isopodichnus* Bornemann, 1889. *Isopodichnus* is highly variable in form with dimorphous traces including small, striated, straight or curved double ribbon trails with a medial furrow and associated or isolated bilobed coffee bean-shaped traces (Häntzschel 1975). At least 13 ichnospecies have been described, generally from nonmarine sediments; these are usually attributed to branchiopod crustaceans. Many of the ichnospecies described are based on compound trace fossils (e.g. *I. osbornei* Glaessner, 1957, and *I. stromnessi* Trewin, 1976). However, despite attempts to distinguish compound traces of *Isopodichnus* from *Cruziana* and *Rusophycus* (Seilacher 1970; Trewin 1976; Pollard 1985; Debriette and Gand 1990; Gand 1994; Gaillard *et al.* 2005; Gaillard and Racheboeuf 2006; Seilacher 2007), arguments for the retention of this ichnogenus rely on invalid ichnotaxobases including producer, size, age and environmental occurrence (Bertling *et al.* 2006). *Isopodichnus* (both *Cruziana*-like and *Rusophycus*-like morphotypes), *Rusophycus* and *Cruziana* are morphologically indistinguishable (Keighley and Pickerill 1996). Therefore, *Isopodichnus* should be abandoned and its ichnospecies transferred to *Cruziana* and *Rusophycus* (Romano and Whyte 1987; Bromley 1990; Keighley and Pickerill 1996; Zonneveld *et al.* 2002; Minter *et al.* 2007*b*). One possible exception is the ichnospecies *Isopodichnus furcosus* Gand, 1994, which is neither *Cruziana*-like nor *Rusophycus*-like, but was transferred to *Rusophycus furcosus* by Minter *et al.* (2007*b*). *I. furcosus* is a small, isolated, horizontal, bilaterally symmetrical, arrow-shaped trace fossil composed of strongly bifurcated ovate lobes with paired divergent longitudinal imprints and associated small internal ovate lobes (Gand 1994). Keighley and Pickerill (1996) suggested that *I. furcosus* may warrant a new ichnogeneric name, a view supported here given the significant morphological difference from *Rusophycus*.

When nomenclature is based on observed morphology alone, excluding all inferences of producer, age, stratigraphic range and facies, names should remain constant through time. Trace fossils with 'major' morphological variation are assigned ichnogeneric status and 'minor' morphological variants considered ichnospecies. Problematically, both major and minor morphological variations may generated by changes in behaviour or preservation (e.g. changes from dry to wet substrate during the production of a trace) (Minter *et al.* 2007*a*). Processes responsible for morphological variation must be understood in order to generate valid names for trace fossils (Minter *et al.* 2007*a*). Although other relationships (e.g. producer or behaviour) can be inferred from trace fossils, they are only ever interpretations. Ethological categories such as Repichnia and Cubichnia as a classification for arthropod traces should be used with caution. An example of the use of behavioural categories in trace fossil classification is the ichnogenus *Pollichianum* Heidtke, 1990. *P. cubichnum* Heidtke, 1990, is an isolated, horizontal, bilaterally symmetrical, flattened pinecone-shaped trace comprising paired lateral, posteriorly orientated, imprints, originating at the mid-line. A second ichnospecies, *P. repichnum* Heidtke, 1990, was proposed for a series of isolated traces, although the individual traces are morphologically identical to *P. cubichnum*. *P. repichnum* therefore essentially represents repeated *P. cubichnum*.

Compound specimens show behavioural variation that grade into each other; for example if *Cruziana* intergrades with *Rusophycus*, they are recognised as ichnotaxa in their own right. But different treatments have been applied to the naming of their compound traces, including naming the whole specimen as one ichnotaxon (Seilacher 1970; Pemberton and Frey 1982; Pickerill 1994; Keighley and Pickerill 1996), i.e. simply as *Cruziana*, while including both ichnotaxa in the description; or naming the compound specimen as a new ichnotaxon (Bertling *et al.* 2006). Previous treatments have resulted in confusion or loss of information; however, if treated as hybrids, as suggested by Minter *et al.* (2007*b*), e.g. *Cruziana* × *Rusophycus*, their inter-relationship is implied. While hybridisation is appropriate for compound specimens, it is unsuitable for so-called complex trace fossils, i.e. trace fossils with multiple components, produced when the organism performs many behaviours sequentially (Bromley *et al.* 2003; Bertling *et al.* 2006). Although the different components may be found separately (and named as valid ichnotaxa), when found together they have distinct morphology and hence may be named as new ichnotaxa (e.g. *Hillichnus lobensis* Bromley *et al.*, 2003, a complex trace fossil produced by a tellinacean bivalve). Composite specimens, the superimposition of one trace fossil on another, are considered invalid ichnotaxa and should be described separately (Bertling *et al.* 2006).

TERMINOLOGY

Descriptive terminology

The terminology used herein is modified primarily from Braddy and Briggs (2002) and Mángano *et al.* (1997); in turn, their definitions were based on Trewin's (1994) descriptive terms for arthropod trackways, modified for the purpose of describing resting traces. An 'imprint' is a discrete mark, while a more continuous mark is termed

an 'impression'. An 'accessory imprint' is an imprint generated by repeated movement (e.g. repositioning of an appendage or limb) of the producer. Accessory imprints are important to distinguish when considering the range of morphology of the trace fossils and interpretation of the producer (e.g. to recognise the types and number of appendages). The 'mid-line' is the medial axis of the trace, while a 'medial imprint' refers to an imprint along the mid-line. The term 'taphoseries' represents a series of ichnotaxa that are extramorphological variants (minor differences in form) resulting from differences in behaviour of the producer or preservation, as introduced by MacNaughton and Pickerill (1995, 2003) and discussed by Minter *et al.* (2007*a*). Lucas (2001) introduced 'taphotaxa', a term to group together morphologically distinct trace fossils generated by taphonomic variation. However, taphoseries already allow for minor variation between forms and 'taphotaxa' are therefore considered invalid (Minter *et al.* 2007*a*).

Ethological terminology

The ethological categories used herein are modified definitions of Seilacher (1964) and Simpson (1975) and are expanded to include the ethological interpretations in Table 1. 'Cubichnia' are traces produced during a temporary halt in locomotion, for resting or refuge, expanded here to include traces produced by animals lying in wait for prey or shallow deposit feeding without forward movement. 'Repichnia' are traces produced by the directed movement of an animal during locomotion (e.g. crawling, walking and running), expanded here to include repeated jumping in a particular direction, and are therefore not always a continuous track or trail. 'Pascichnia' are traces produced during the combination of feeding and locomotion (grazing traces). 'Fugichnia' are escape reaction traces in response to a sudden sediment influx. 'Volichnia' are the discrete traces made by the landing and take-off of flying animals.

GEOLOGICAL SETTING

The ichnofossils documented herein were collected from the lower part of the Early Jurassic Blue Lias Formation at Southam Cement Works Quarry near Long Itchington, Warwickshire in Central England (National Grid Reference SP 418630) (Text-fig. 1). The geology of this site has been summarised by Old *et al.* (1987), Ambrose (2001) and Radley (2002, 2008) and comprises formerly exposed strata of Late Triassic to Early Jurassic age (Text-fig. 2). Much of the quarry is now flooded and largely inaccessible.

Triassic (Rhaetian) strata, formerly seen in the quarry floor, comprise the marginal marine Cotham and Langport Members of the Lilstock Formation (Swift 1995; Radley 2002). Overlying an eroded surface of Langport Member limestone, the Early Jurassic (Hettangian) Blue Lias Formation is represented by the Saltford Shale and Rugby Limestone Members (Liasicus to Bucklandi Chronozone; Ambrose 2001).

The Saltford Shale Member (Liasicus to Angulata Chronozone; approximately 17-m thick) is dominated by dark-grey laminated mudstone with a few thin beds of fine-grained limestone. The mudstones additionally enclose lenticles and nodules of calcareous siltstone, some representing scour and gutter casts. The generally sparse macrofauna of the Saltford Shale is dominated by schlotheimiid ammonites, nautiloids, fish debris and reptile remains, occasionally concentrated as gutter and scour-fills (Radley 2002, 2008; Smith and Radley 2007). Rare macrobenthos includes sparse occurrences of small bivalves, possibly nuculoideans. Towards the top of the Saltford Shale, reworked limestone nodules and intercalations of bivalve and echinoid debris signal the transition to the overlying Rugby Limestone Member, the classic 'Blue Lias' facies of relatively fossiliferous, benthos-rich, bioturbated argillaceous limestones and mudstones (Ambrose 2001).

Regionally, the Saltford Shale Member is strongly transgressive (Donovan *et al.* 1979) and confirms the establishment of a sea over the English Midlands in the Early Jurassic. The laminated, benthos-poor nature of much of the succession indicates an essentially dysaerobic to anoxic setting, possibly interspersed with relatively oxic phases during deposition of fine-grained limestone beds (Radley 2003*a*). Weak storm flows are thought to be responsible for generating the scour and gutter casts. Comparison with the lateral and bathymetric distribution of similar storm-deposited sediments in modern shelf seas suggests depths of no more than a few tens of metres (Hallam 1997). Above the Saltford Shale Member, the Rugby Limestone Member marks increased benthic oxygenation, possibly linked to shallowing (Radley 2002, 2008; Smith and Radley 2007).

The horizon of interest for this study lies approximately 7 m above the base of the Saltford Shale Member where a concentration of calcareous siltstone lenticles representing shallow scour-fills preserves the suite of trace fossils in hyporelief and epirelief. The lenticles are up to 205 mm long and 15 mm thick. The generally uneven, undulating, lower surfaces preserve shallow flute casts and minute, disarticulated bivalve shells. Framboidal pyrite concretions are clustered on the lower surfaces of the lenticles. The lenticles frequently display some upward-coarsening in the silt grain size and their upper surfaces are relatively flat.

TEXT-FIG. 1. Maps showing the location of Warwickshire, central England and the distribution of the Jurassic outcrop (modified from Radley 2005). The location of Southam Cement Works Quarry is marked with a star and the inset map shows the location of the quarry (redrawn from Radley 2002).

The ichnofauna of the Southam Cement Works Quarry has been mentioned previously by Clements (1975), Barras (2002), Barras and Twitchett (2007) and Radley (2008). The new trace fossils herein were informally assigned to *Cruziana* or *Isopodichnus*, by Barras (2002), Radley (2002) and Barras and Twitchett (2007). Four ichnogenera, *Arenicolites*, *Diplocraterion*, *Palaeophycus* and *Rhizocorallium* have been noted from the Rhaetian Langport Member. Other records of trace fossils from the Saltford Shale are restricted to shallow-tier bioerosion traces on limestone clasts in a basal pebble bed and within a discrete horizon approximately 12 m above the base and a restricted *Chondrites* ichnofauna in the upper beds (Radley 2008). The overlying Rugby Limestone Member is extensively bioturbated (Clements 1975; Radley 2002; Barras and Twitchett 2007).

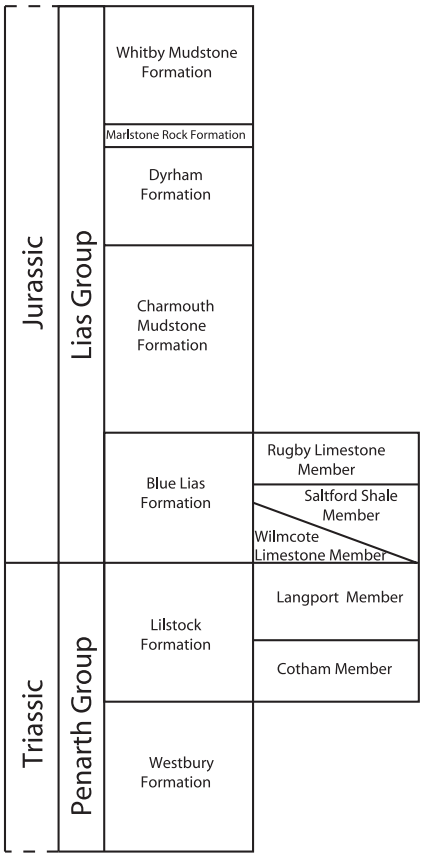
SYSTEMATIC PALAEONTOLOGY

Ichnogenus SOLUSICHNIUM nov.

Derivation of name. Latin, *solus*, only; *ichn,* trace; *ium*, little, with reference to this little trace fossil being the only known evidence of macrobenthic activity at this level in the Saltford Shale Member.

Type ichnospecies. Solusichnium southamensis isp. nov.

Diagnosis. Small, bilaterally symmetrical, isolated traces with elongated suboval outline. Anterior and middle regions are concave in relief with internal convex imprints; posteriorly the relief is subtly to noticeably convex. Clearly defined anterior region, semicircular to



TEXT-FIG. 2. Outline stratigraphy of the Upper Triassic and Lower Jurassic succession in Warwickshire, central England (adapted from Radley 2003*a*, *b*).

arrow-shaped in outline. Two pairs of linear imprints project anteriorly from the anterior edge. A medial imprint in the middle region thickens and splits anteriorly, joining one long linear imprint pair. The second, much shorter pair has a more distal position, when present. Lateral imprints extend from either side of the distal anterior region and curve posteriorly with bifurcating terminations. Middle region is elongate and narrows posteriorly with internal transverse to posteriorly orientated imprints thinning towards the posterior region, cross-cut by the medial imprint. Posterior region tapers posteriorly and terminates with globular V-shaped imprints.

Solusichnium southamensis isp. nov.
Text-figures 3–5

2002 *Isopodichnus* Radley, p. 172
2002 *Isopodichnus* and *Selenichnites* Barras, p. 52, pl. 2
2007 *Cruziana* Barras and Twitchett, p. 231

Derivation of name. Southam, the name of the nearest town to the quarry, from which the specimens were collected. Latin, *ensis*, belonging to.

Holotype. WARMS: G 15641, Text-figure 3A.

Paratypes. WARMS: G 15763/58, WARMS: G 156763/57, WARMS: G 15763/11, WARMS: G 15763/39, deposited in the collections of the Warwick Museum, Warwickshire, central England.

Other material. WARMS: G 15525/1A–C, WARMS: G 15746, WARMS: G 15763/1–10, WARMS: G 15763/12–38, WARMS: G 15763/40–56, WARMS: G 15763/59–60.

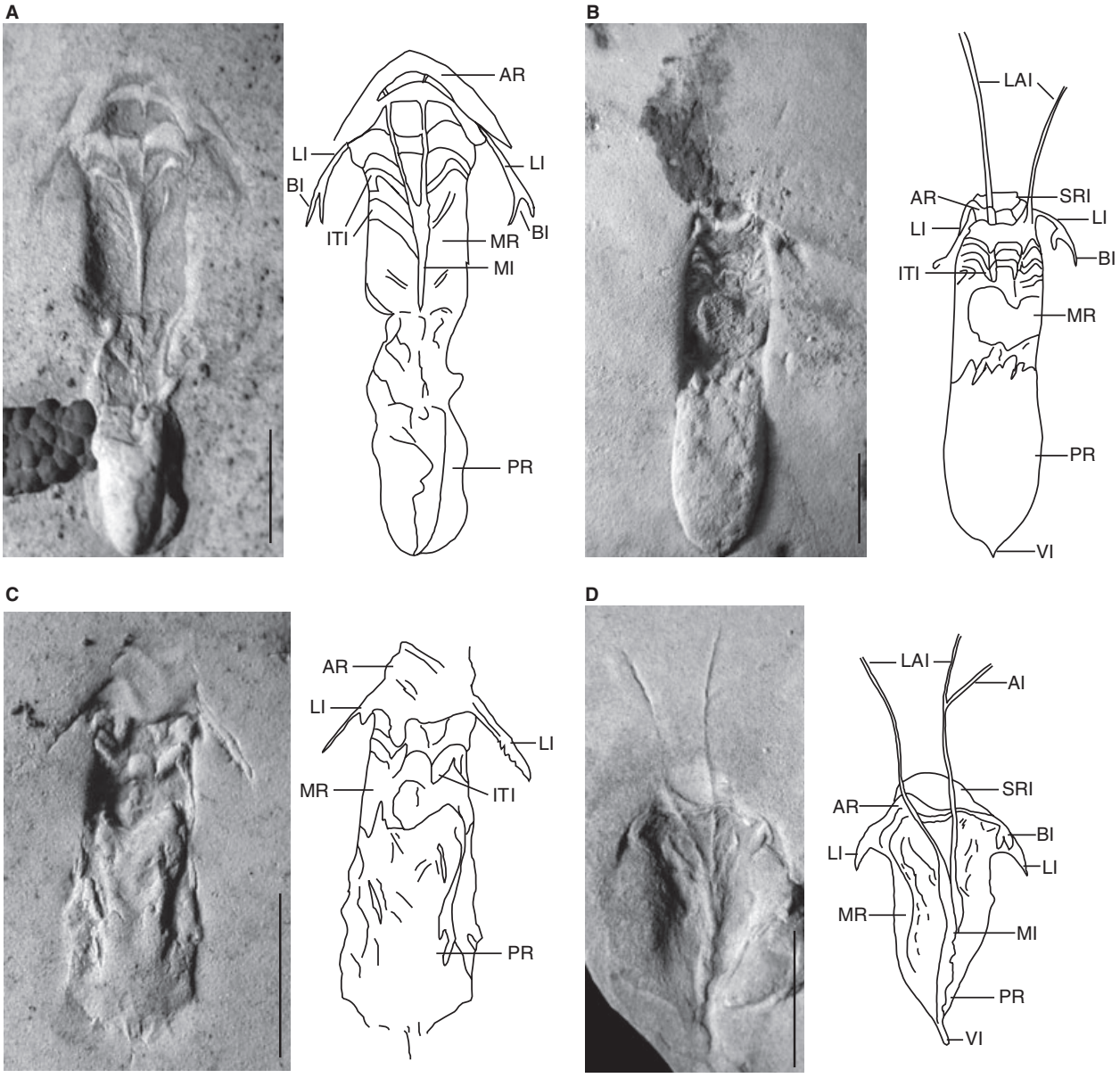
Locality and age. A lenticular siltstone horizon 7 m above the base of the Saltford Shale Member of the Blue Lias Formation (Early Jurassic; Liasicus to Angulata Chronozone), Southam Cement Works Quarry near Long Itchington, Warwickshire in central England (National Grid Reference SP 418630).

Diagnosis. As for ichnogenus.

Description. Small, bilaterally symmetrical, elongate suboval isolated traces. These traces have unusual relief, all hypichnial, but preserved with convex imprints within the overall concave relief in the anterior and middle regions, with a transition into fully convex in the posterior region. The traces vary in size, with the best preserved complete specimens up to 57 mm long and 20 mm wide; most are smaller and incomplete.

A clearly defined anterior region is semicircular in outline; a small number of variants also preserve a subtle subrectangular imprint projecting anteriorly from the more obvious anterior outline (Text-fig. 3C–D). Two pairs of linear imprints project anteriorly away from the anterior edge, but specimens rarely have both pairs of linear imprints preserved (Text-figs 3C–D, 4A–C, 5B). When present, the longer pair is of similar length to the total length of the anterior and middle regions; in one specimen (WARMS: G 15763/57) one of the imprints has a small bifurcation near the most anterior end (Text-fig. 3D). Lateral imprints extend from either side of the distal anterior region and curve posteriorly with bifurcating terminations. Bifid lateral extensions are seen in the best preserved forms (WARMS: G 15641, WARMS: G 15763/58, WARMS: G 15763/57, Text-fig. 3A–B, D) and without them the overall outline becomes subrectangular. One morphotype (WARMS: G 15525/2) displays a second bifid imprint on one side in the anterior region (Text-fig. 4D). Other variants with poorly developed anterior and posterior regions, may exhibit paired lateral extensions from the anterior, posterior or centre of the middle region.

The middle region is elongate and narrows posteriorly with internal transverse to posteriorly orientated imprints, narrowing towards the posterior region, cross-cut by the medial imprint. In many specimens the middle area is well defined but internal features are poorly preserved. In a few specimens (e.g. WARMS: G 15763/14), the outline is poorly developed but posteriorly orientated imprints create a mottled appearance in the middle region (Text-fig. 5A). The posterior region tapers posteriorly and terminates with globular V-shaped imprints in well-preserved specimens (e.g. WARMS: G 15746, WARMS: G 15763/58, WARMS: G 15763/57, Text-figs 3B, D, 4B). Some

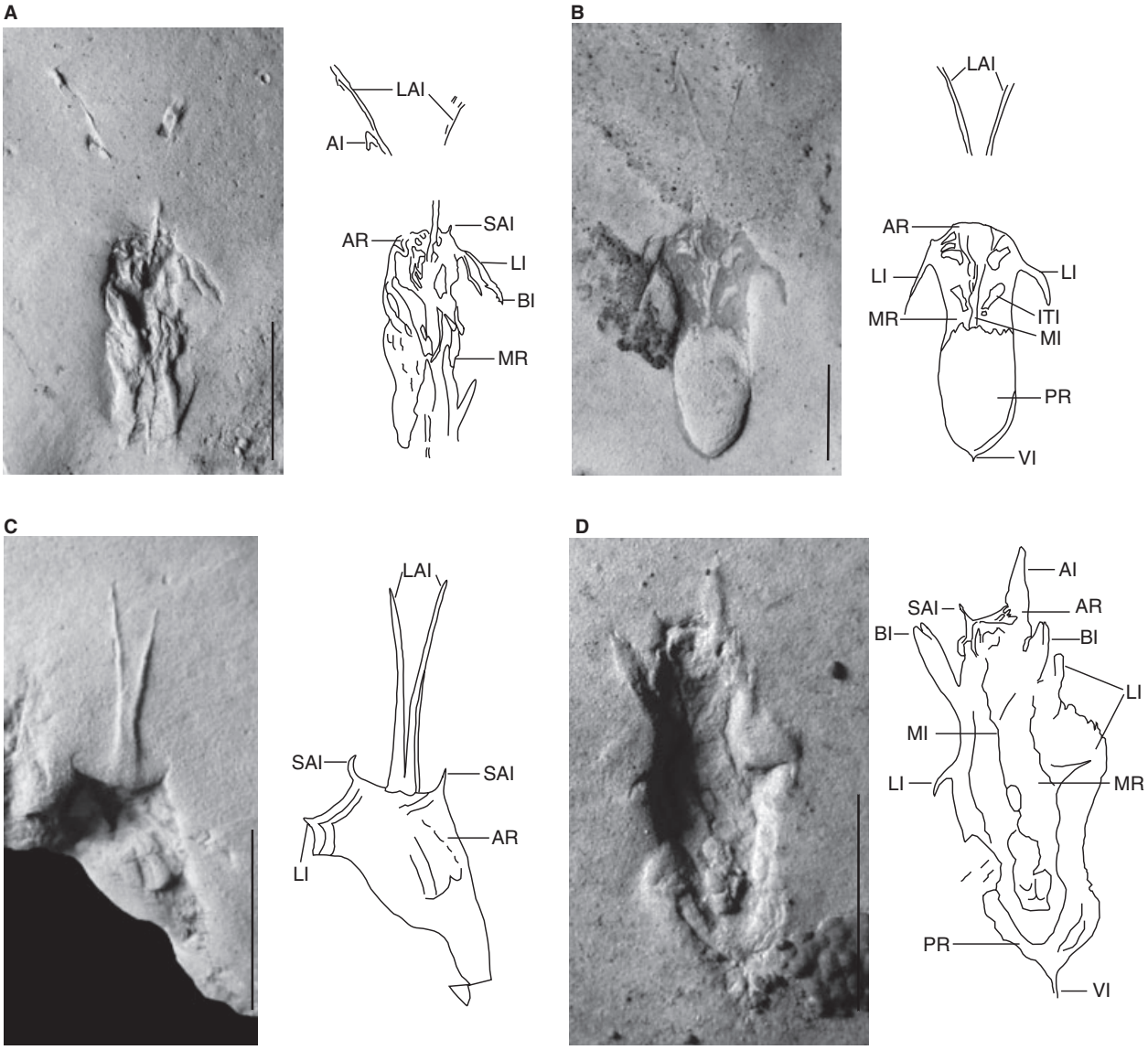


TEXT-FIG. 3. A–D, photographs and line drawings showing the morphological variation of *Solusichnium southamensis* igen. et isp. nov., all hypichnial. A, holotype, WARMS: G 15641. B, paratype, WARMS: G 15763/58. C, WARMS: G 15525/1A. D, paratype, WARMS: G 15763/57. Scale bars 10 mm. Abbreviations: AR, anterior region; MR, middle region; PR, posterior region; SRI, subrectangular imprint; LAI, long anterior imprint; SAI, short anterior imprint; AI, accessory imprint; LI, lateral imprint; BI, bifid imprint; MI, medial imprint; ITI, internal transverse imprint; VI, V-shaped imprint.

morphotypes have V-shaped imprints at the posterior end when preserved without the convex mound structure. The V-shaped imprints may be repeated posteriorly to form a series. The traces may be isolated on the slabs or occur as cross-cutting groups, accompanied by modification to previously formed traces.

Remarks. Superficially, poorly preserved shallow specimens of *S. southamensis* with overlapping striations are similar to *Rusophycus*, but lack the well-developed parallel lobes more typical of the latter.

Solusichnium southamensis is divided into three regions longitudinally, a feature also found in *Tripartichnus* Vallon and Röper, 2006. *T. triassicus* Vallon and Röper, 2006, has a similar overall morphology with a semicircular anterior region, elongate middle region and V-shaped posterior region, although the regions are clearly separated and do not intergrade as in *S. southamensis*. The linear imprints and internal morphology are absent in *T. triassicus*. *T. imbergi* Vallon and Röper, 2006, however, does have long linear anterior imprints, but has distinctly

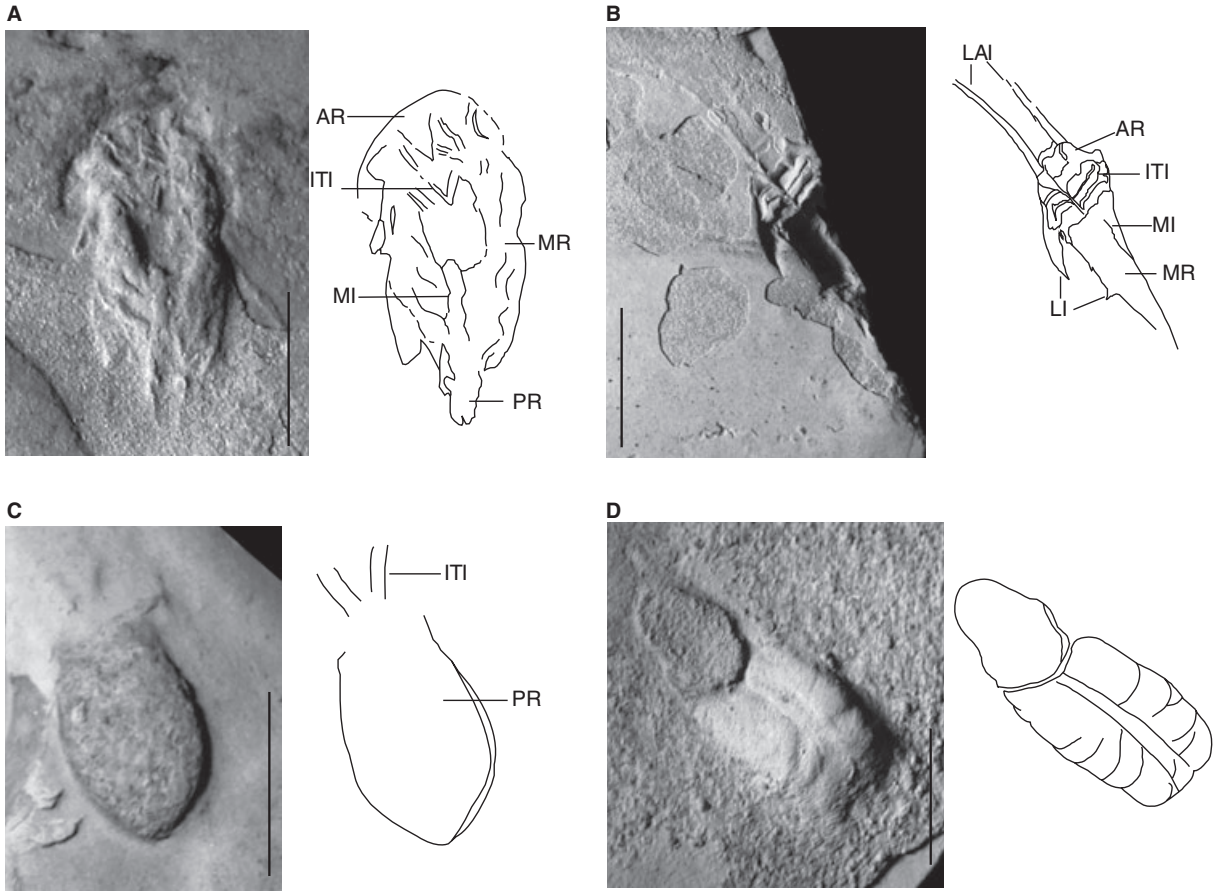


TEXT-FIG. 4. A–D, photographs and line drawings showing the morphological variation of *Solusichnium southamensis* igen. et isp. nov., all hypichnial. A, WARMS: G 15763/37. B, WARMS: G 15746. C, paratype, WARMS: G 15763/11. D, WARMS: G 15525/2. Scale bars 10 mm. See Text-figure 3 for abbreviations.

separate regions, with the posterior region elongate and rounded.

Kingella natalensis Savage, 1971, is a small, isolated, horizontal, bilaterally symmetrical trace with an elongate, clearly defined, serrate oval outline. There are two pairs of linear imprints anteriorly and four pairs of lateral imprints extending posteriorly almost parallel to the mid-line. *S. southamensis* is also somewhat similar to *K. natalensis*, in that it has two pairs of anterior linear imprints, although these are much shorter in proportion to the main body imprint in the latter. However, *K. natalensis* lacks the three distinct regions of *S. southamensis* and although it has paired imprints internally, they are situated almost longitudinally a short distance either side of the mid-line; no imprints are bifid or extend laterally.

Solusichnium southamensis is similar to a paratype (AMNH 42696) of *Chagrinichnites osgoodi* Hannibal and Feldmann, 1983, in its shape and relief, with a concave anterior region, a convex subtriangular posterior region (although preserved in epirelief) and a lateral imprint (evident *in* Hannibal and Feldmann 1983, p. 708, fig 2A, although not mentioned in the description). This paratype is the only epirelief specimen figured in the original description of *C. osgoodi* and is unlike the morphology of the hyporelief specimens, which typically have a wide ovoid anterior region, narrowing in the middle and wid-



TEXT-FIG. 5. A–C, photographs and line drawings showing the morphological variation of *Solusichnium southamensis* igen. et isp. nov., all hypichnial. D, photograph and line drawing of *Rusophycus* isp. indet., epichnial. A, WARMS: G 15763/14. B, paratype, WARMS: G 15763/39. C, WARMS: G 15763/16. D, WARMS: G 15763/60. Scale bars 10 mm. See Text-figure 3 for abbreviations.

ening posteriorly into a well-developed *Rusophycus*-like region. Although the traces on the upper and lower surfaces were produced by the same animals and clearly demonstrated to be linked by the bioturbation of the sediment layers between them during the production of these escape traces (Hannibal and Feldmann 1983), the morphologies are distinctly different and considered here to represent a compound trace fossil rather than the same ichnotaxon. The morphological differences between the paratype (AMNH 42696) and the other types of *C. osgoodi* may warrant separate ichnogeneric assignment. Epichnial *C. osgoodi* may be more similar to poorly preserved *S. southamensis* than the hypichnial *C. osgoodi*, although it lacks the distinct internal detail and lateral imprints.

Associated trace fossils. The hypichnial *S. southamensis* traces often occur with similarly orientated epichnial *Rusophycus* isp. indet. traces (e.g. WARMS: G 15763/60, Text-fig. 5D). The overlying *Rusophycus* traces are not vertically above the *S. southamensis*, but offset anteriorly by up to 20 mm. These traces (up to 16 mm long and 10 mm wide) are isolated, parallel bilobed and coffee bean-shaped, exhibiting transverse striations. They are preserved in convex epirelief and are sometimes associated with a low flat oval positive relief structure. *Rusophycus* is usually preserved in convex hyporelief or concave epirelief (Keighley and Pickerill 1996), and this very unusual preservation of convex epirelief has not been reported previously. Although there is no direct evidence that the *S. southamensis* traces are linked to the *Rusophycus* traces (i.e. evidence of disturbed laminations), given the proximity and orientation of the two, it can be inferred that they represent a compound trace (i.e. *Solusichnium* × *Rusophycus*). *Rusophycus* is generally attributed to shallow digging by trilobites or other arthropods for the purposes of feeding, hiding or resting. Given the unusual relief of the *Rusophycus* described here, an alternative method of production is proposed.

DISCUSSION

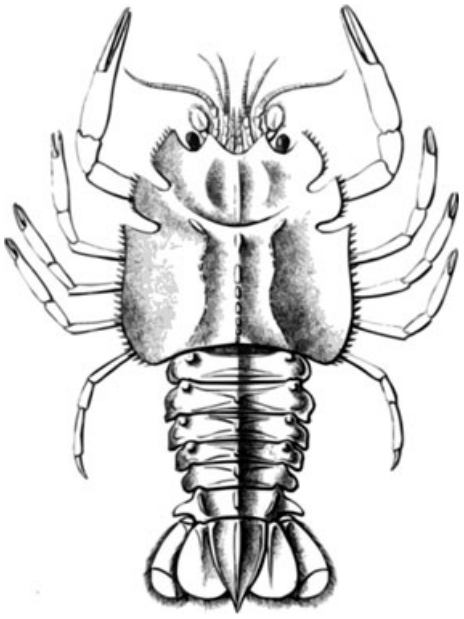
Potential producers

The *S. southamensis* trace fossils are sufficiently detailed that they express the ventral anatomy of their producer. The shape of the traces is consistent with an arthropod

producer, divided into three distinct regions representing tagma (i.e. head, abdomen and tail). The lateral imprints reflect paired appendages. The paired anterior linear imprints are interpreted as representing two pairs of antennae, one very long and narrow (first antennae) and the second much shorter and broader (antennules) (Text-fig. 4C). The anterior region is broadly curved and clearly defined, suggesting a sclerotized carapace. The pair of laterally extending bifid imprints are interpreted as the marks of chelate appendages. A possible second pair in one morphotype (WARMS: G 15525/2, Text-fig. 4D) may represent readjustments of the position of these appendages or a second pair of chelate appendages; the former is favoured here.

The two pairs of antennae and chelate appendages indicate a decapod crustacean producer. The proportions of the trace (length twice its width) and the small chelipeds, relative to the overall size of the animal, imply a lobster-like producer. The subtle semicircular imprint at the anterior margin on some morphotypes might imply the presence of a rostrum, also a feature of decapods. The accessory imprints of the middle region are interpreted as abdominal appendage marks. They do not extend beyond the lateral edge of the middle region, implying that these appendages were short or tucked in tightly under the body. Consequently, they are interpreted as representing the pleopods. The V-shaped posterior imprint is interpreted as a telson mark. Primitive decapods have V-shaped pointed telsons and lack diaeresis (axial cuticle thickening) in the uropods (Glaessner 1969), which may explain why the remainder of the tail mark is not preserved.

While body fossils of a nektonic fauna occur in the Saltford Shale Member, macrobenthos is sparse. The Rhaetian–basal Hettangian Wilmcote Limestone Member underlies the Saltford Shale in the Avon Valley of south-western Warwickshire, but is absent in the Southam area (Ambrose 2001). The upper part of the member is developed largely as laminated limestone-shale facies. Like the Saltford Shale at Southam, fossils of macrobenthos are virtually absent in these beds, similarly indicating anoxic or dysaerobic conditions (Simms *et al.* 2004). Perhaps significantly, there are several records of intact decapod crustaceans (Woodward 1866; Brodie 1868; Woods 1925–31). Woodward (1866) described and figured two decapods, *Eryon wilmcotensis* and *Aeger brodei*, from the 'bottom blocks' of the Wilmcote Limestone, a limestone unit 1 m below the base of the Saltford Shale at its type locality in the Newnham (Wilmcote) Quarry, south-western Warwickshire (National Grid Reference SP 151594; Simms *et al.* 2004). Brodie (1868) described the Wilmcote Limestone Member 'insect and saurian' beds at Wilmcote, noting numerous *Eryon wilmcotensis*, as well as a species of *Astacus* and *Eryon barrovensis.* Woodward



TEXT-FIG. 6. *Eryon barrovensis*, a potential producer of *Solusichnium southamensis* igen. et isp. nov., from the Wilmcote Limestone Member of Warwickshire, specimen is 124 mm long, reproduced from Woodward (1866, pl. 25, fig. 1).

(1893, pp. 151–152) recorded *Eryon barrovensis* and *Eryon wilmcotensis* in the upper part of the Wilmcote Limestone Member at Wilmcote. Woods (1925–31) also noted these taxa in the Wilmcote Limestone Member and also *Coleia barroviensis*, which he considered to be synonymous with *Coleia (Eryon) wilmcotensis*. The only description available of these Wilmcote decapods is by Woodward (1866). *Eryon barrovensis* McCoy, 1849, (Text-fig. 6) has a flat carapace with a truncated posterior margin and spinose lateral margins with two lateral indentations on each side and an acutely triangular telson. *Eryon wilmcotensis* Woodward, 1866, is very similar but smaller (the largest specimen is 50 mm long and 18 mm wide), although only its carapace has been figured and the size of the appendages is unknown. An *Eryon*-like decapod crustacean is, therefore, considered the possible producer of *S. southamensis*, as the size and morphology of each is comparable. Given the proximity and orientation of the overlying *Rusophycus* isp. indet. traces, it is suggested that they were also made by the same producer. Simms *et al.* (2004) suggested that the Wilmcote decapods were not necessarily benthic because of the anoxic to dysaerobic conditions.

Palaeoecological implications

As discussed earlier, the benthic conditions of the Saltford Shale Member are thought to have been dysaerobic to anoxic, interrupted by weak storm flows. It is suggested

that the decapods were essentially epibenthic, but were disturbed by these weak storm flows and buried beneath rapidly deposited silt. The suite of traces was thus produced when these decapods moved upwards through the sediment. The excellent preservation of the hypichnial traces suggests these decapods may have sheltered beneath the silt, while the storm flow abated. The thrusting of the appendages into the sediment and the beating of the tail would have aided movement up through the sediment and resulted in the globular V-shaped posterior traces. Flume tank experiments conducted with spiny lobsters have shown that when subject to sudden water movement or obstacles, they use rapid flicks of their abdomen and tail as a rapid reverse escape reaction or cling to the floor of the tank (Jeffs and Holland 2000).

Exit onto the upper surface of the silt is recorded by the *Rusophycus* isp. indet. traces, possibly made by the carapace as the arthropods emerge onto the substrate (Text-fig. 5D). There is no published example of this type of convex epichnial relief; this implies a new behavioural interpretation of *Rusophycus*. This is especially important as *Rusophycus* has been used as a palaeoenvironmental indicator and to determine the way-up of bedding. If these *Rusophycus* trace fossils were found in isolation without underlying *S. southamensis*, their palaeoecological significance may not have been appreciated.

Not every specimen of *S. southamensis* has a corresponding *Rusophycus* specimen, and there are two possible explanations for this: The first is taphonomic, i.e. the *Ruspohycus* has a lower preservation potential to the underlying *S. southamensis* as it was formed at the sediment water interface. Alternatively, if the decapods were sheltering from the storm conditions, they may have moved off the sediment surface before being buried by storm flows. Therefore, some *S. southamensis* specimens may be resting traces only and not escape traces.

Taphoseries

The large sample size and range of trace morphologies allows the identification of a taphoseries. The taphoseries results from preservational and behavioural variation with many isolated traces showing only partial elements of the diagnosis. Recognition of such taphoseries is important in ichnotaxonomy, most obviously as it prevents unwarranted proliferation of names. The range of taphonomic variants of *S. southamensis* does not generate a series of variants that grade into each other (i.e. progressively from best to worst preserved). Instead, specimens display different preservational states where particular features are absent or present. This morphological variation results from different combinations of taphonomic bias and subtle behavioural variation.

Solusichnium southamensis has five general morphotypes. Type 1 preserves the greatest amount of detail, showing the majority of the internal details (e.g. bifurcated imprints, medial imprint and transverse imprints) and an external outline with a well-preserved posterior region (e.g. WARMS: G 15641, WARMS G 15763/58, Text-fig. 3A–B). Type 2 has poorer preservation, with partial loss of both internal details and external outline (e.g. WARMS: G 15763/57, WARMS: G 115763/37, WARMS: G 15746, Text-figs 3D, 4A–B). This type still retains most details, although the posterior area is poorly developed, and imprints of the chelate appendages show no evidence of bifurcation. Type 3 has almost complete loss of posterior and anterior details. These specimens lack the deep concave hyporelief of the previous types (e.g. WARMS: G 15525/1A, WARMS: G 15525/2, WARMS: G 15763/14, Text-figs 3C, 4D, 5A). They are mottled in appearance and are preserved best in the middle region. The poorer quality of preservation may be taphonomic or may reflect the producer having settled less deeply into the sediment than in other types. Type 4 has a clearly defined outer region, but lacks internal detail. These traces generally have deep relief and show good detail in the anterior region (e.g. WARMS: G 15763/11, WARMS: G 15763/16, Text-Figs 4C, 5C). Enhanced preservation of anterior features may reflect how the producer interacted with the sediment. The internal features may have been lost because of subsequent movement (overprinting). Type 5 has no details other than a well-developed convex hyporelief posterior section (e.g. WARMS: G 15763/60, Text-fig. 5D). No internal details are evident, and the general outline is lost. This may result from overprinting, or the ventral anatomy of the producer may not have been in contact with the sediment surface.

CONCLUSIONS

A new suite of arthropod trace fossils is described from the Lower Jurassic Saltford Shale consisting of hypichnial *Solusichnium southamensis* igen. et isp. nov. and epichnial *Rusophycus* isp. indet. traces.

Solusichnium southamensis consists of isolated, small, bilaterally symmetrical, suboval hypichnia, comprising three regions. The features of the trace fossils have been demonstrated to be the imprints of laterally extended chelate appendages and imprints of antennae and antennules, which extended anteriorly. The elongate middle region contains appendage imprints that extend laterally and the convex posterior region terminates in a globular V-shaped imprint representing the telson.

Solusichnium southamensis reflects the ventral anatomy of its producer, interpreted as an *Eryon*-like decapod

similar to those found in the slightly older Wilmcote Limestone. The Wilmcote Limestone is demonstrated to have a similar palaeoenvironment as the Saltford Shale and the smaller of the *Eryon* species, *Eryon wilmcotensis*, is consistent with the size of these trace fossils. There are, thus, palaeoecological, as well as morphological grounds, for associating *S. southamensis* with the Wilmcote taxa.

The suite of trace fossils is found on siltstone lenses in what is otherwise a laminated mudstone unit and interpreted as the escape reactions of these small decapods when smothered by a distal storm deposit. The hypichnial traces are resting traces of these decapods possibly when they took refuge on the sea floor during storm events. Following chance burial by storm flow deposits, the epichnial traces are envisaged as being formed as the decapods exited onto the upper surface of the silt layer. The ethology of the *S. southamensis* fossils is, therefore, Cubichnia (resting traces), and where present in concurrence with *Rusophycus* traces, their compound traces are considered to be Fugichnia (escape traces).

The interpretation of the *Rusophycus* traces as the exit marks of these decapods is a new interpretation of *Rusophycus* and has interesting palaeoecological implications for this group of trace fossils. Therefore, not all *Rusophycus* trace fossils can be assumed to be resting traces and urges caution for the use of *Rusophycus* as palaeoenvironmental indicators.

Acknowledgements. The authors thank the anonymous reviewer, C. Gaillard and P. Orr for their constructive comments on an early version of the manuscript. We also thank Cemex UK for allowing collection of specimens from the Southam Cement Works Quarry.

REFERENCES

AMBROSE, K. 2001. The lithostratigraphy of the Blue Lias Formation (Late Rhaetian–Early Sinemurian) in the southern part of the English Midlands. *Proceedings of the Geologists' Association*, **112**, 97–110.

BARRAS, C. G. 2002. The effects of the end-Triassic mass extinction on the ichnofossil record. Unpublished MSc Thesis, University of Bristol, Bristol, 90 pp.

—— and TWITCHETT, R. J. 2007. Response of the marine infauna to Triassic-Jurassic environmental change: Ichnological data from southern England. *Palaeogeography, Palaeoclimate, Palaeoecology*, **244**, 223–241.

BENNER, J. S., RIDGE, J. C. and TAFT, N. K. 2008. Late Pleistocene freshwater fish (Cottidae) trackways from New England (USA) glacial lakes and a reinterpretation of the ichnogenus *Broomichnium* Kuhn. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **260**, 375–388.

BERTLING, M., BRADDY, S. J., BROMLEY, R. G., DEMATHIEU, G. R., GENISE, J., MIKULÁŠ, R., NIELSEN, J. K., RINDSBERG, A. K., SCHLIRF, M. and UCHMAN, A. 2006. Names for trace fossils: a uniform approach. *Lethaia*, **39**, 265–286.

BORNEMANN, J. G. 1889. Über den Buntsandstein in Deutschland und seine Bedeutung für die Trias. *Beiträge zur Geologie und Paläontologie*, **1**, 1–61.

BRADDY, S. J. and BRIGGS, D. E. G. 2002. New Lower Permian nonmarine arthropod trace fossils from New Mexico and South Africa. *Journal of Paleontology*, **76**, 546–557.

BRODIE, P. B. 1868. A sketch of the Lias generally in England and of the "Insect and Saurian beds", especially in the lower division in the counties of Warwick, Worcester and Gloucester, with a particular account of the fossils which characterize them. *Proceedings of the Warwickshire Naturalists' and Archaeologists' Field Club*, **1868**, 1–24.

BROMLEY, R. G. 1990. Trace fossils: biology and taphonomy. *Special topics in palaeontology, 3*. Unwin Hyman, London, 280 pp.

——UCHMAN, A., GREGORY, M. R. and MARTIN, A. J. 2003. *Hillichnus lobosensis* igen. et isp. nov., a complex trace fossil produced by tellinacean bivalves, Paleocene, Monterey, California, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **192**, 157–186.

BUATOIS, L. A., MÁNGANO, M. G., GENISE, J. F. and TAYLOR, T. N. 1998. The ichnologic record of the invertebrate invasion of nonmarine ecosystems: Evolutionary trends in ecospace utilization, environmental expansion, and behavioral complexity. *Palaios*, **13**, 217–240.

CALLISON, G. 1970. Trace fossils of trilobites from the Deadwood Formation (Upper Cambrian) of western South Dakota. *Bulletin of the Southern California Academy of Sciences*, **69**, 20–26.

CLEMENTS, R. G. 1975. *Report on the geology of Long Itchington Quarry (Rugby Portland Cement Company Limited, Southam Works, Long Itchington, Warwickshire)*. Department of Geology, University of Leicester, Leicester.

CRIMES, T. P. 1975. The stratigraphical significance of trace fossils. 109–130. *In* FREY, R. W. (ed.). *The study of trace fossils*. Springer Verlag, New York, 562 pp.

DEBRIETTE, P. and GAND, G. 1990. Conséquences stratigraphiques et paléoenvironnementales de nouvelles observations paléontologiques dans le Permien de la partie occidentale du bassin de Lodève (Sud du Massif Central). *Géologie de la France*, **1**, 19–32.

DONOVAN, D. T., HORTON, A. and IVIMEY-COOK, H. C. 1979. Transgression of the Lower Lias over the northern flank of the London Platform. *Journal of the Geological Society, London*, **136**, 165–173.

FELDMANN, R. M., OSGOOD, R. G., Jr, SZMUC, E. J. and MEINKE, D. W. 1978. *Chagrinichnites brooksi*, a new trace fossil of arthropod origin. *Journal of Paleontology*, **52**, 287–294.

FISCHER, W. A. 1978. The habitat of the early vertebrates: trace and body fossil evidence from the Harding Formation (Middle Ordovician), Colorado. *The Mountain Geologist*, **15**, 1–26.

FORTEY, R. A. and SEILACHER, A. 1997. The trace fossil *Cruziana semiplicata* and the trilobite that made it. *Lethaia*, **30**, 105–112.

GAILLARD, C. and RACHEBOEUF, P. R. 2006. Trace fossils from nearshore to offshore environments: Lower Devonian of Bolivia. *Journal of Paleontology*, **80**, 1205–1226.

—— HANTZPERGURE, P., VANNIER, J., MARAGERARD, A. and MAZIN, J. 2005. Isopod trackways from the Crayssac Lagerstatte, Upper Jurassic, France. *Palaeontology*, **48**, 947–962.

GAND, G. 1994. Ichnocoenoses à *Isopodichnus furcosus* nov. ichnosp. dans le Permien du Bassin de Lodève (Massif Central, France). *Geobios*, **27**, 73–86.

GLAESSNER, M. F. 1957. Palaeozoic arthropod trails from Australia. *Paläontologische Zeitschrift*, **31**, 103–109.

—— 1969. Decapoda. *In* MOORE, R. C. and TEICHERT, C. (eds). *Treatise on invertebrate paleontology. Part R. Arthropoda 4, Volume 2*. Geological Society of America, Boulder and University of Kansas Press, Lawrence, 651 pp.

HALLAM, A. 1997. Estimates of the amount and rate of sea-level change across the Rhaetian–Hettangian and Pliensbachian–Toarcian boundaries (latest Triassic to early Jurassic). *Journal of the Geological Society, London*, **154**, 773–779.

HANNIBAL, J. T. and FELDMANN, R. M. 1983. Arthropod trace fossils, interpreted as Echinocarid escape burrows, from the Chagrin Shale (Late Devonian) of Ohio. *Journal of Paleontology*, **57**, 705–716.

HÄNTZSCHEL, W. 1975. Trace fossils and problematica. W1–W269. *In* MOORE, R. C. and TEICHERT, C. (eds). *Treatise on invertebrate paleontology. Part W. Miscellanea*. Geological Society of America, Boulder and University of Kansas Press, Lawrence, 269 pp.

HARDY, P. G. 1970. New xiphosurid trails from the Upper Carboniferous of northern England. *Palaeontology*, **13**, 188–190.

HEIDTKE, U. 1990. *Pollichianum cubichnum* nov. ichnogen. et ichnospec. und *Pollichianum repichnum* nov. ichnospec., zwei neue Invertebratenichnia aus dem saar-pfälzischen Rotliegend (Unter-Perm, SW-Deutschland). *Mitteilungen der Pollichia*, **77**, 133–139.

HESSELBO, S. P. 1988. Trace fossils of Cambrian aglaspidid arthropods. *Lethaia*, **21**, 139–146.

HOLUB, V. and KOZUR, H. 1981. Arthopodenfährten aus dem Rotliegenden der CSSR. *Geologisch-Paläontologische Mitteilungen Innsbruck*, **11**, 95–148.

JEFFS, A. G. and HOLLAND, R. C. 2000. Swimming behaviour of the puerulus of the spiny lobster, *Jasus ewardsii* (Hutton, 1875) (Decapoda, Palinuridae). *Crustaceana*, **73**, 847–856.

KEIGHLEY, D. G. and PICKERILL, R. K. 1996. Small *Cruziana*, *Rusophycus*, and related ichnotaxa from eastern Canada: the nomenclatural debate and systematic ichnology. *Ichnos*, **4**, 261–285.

KUHN, O. 1958. *Die Fährten der Vorzeitlichen Amphibien und Reptilien*. Meisenbach KG, Bamberg.

LUCAS, S. G. 2001. Taphotaxon. *Lethaia*, **34**, 30.

MACNAUGHTON, R. B. and PICKERILL, R. K. 1995. Invertebrate ichnology of the nonmarine Lepreau Formation (Triassic), southern New Brunswick, eastern Canada. *Journal of Paleontology*, **69**, 160–171.

—— —— 2003. Taphonomy and the taxonomy of trace fossils: a commentary. *Lethaia*, **36**, 66–70.

MÁNGANO, M. G., BUATOIS, L. A., MAPLES, C. G. and LANIER, W. P. 1997. *Tonganoxichnus*, a new insect trace from the Upper Carboniferous of eastern Kansas. *Lethaia*, **30**, 113–125.

MARTIN, A. J. 2006. Resting traces of *Ocypode quatrata* associated with hydration and respiration: Sapelo Island, Georgia, USA. *Ichnos*, **13**, 57–67.

MCCOY, F. 1849. On the classification of some British fossil Crustacea, with notices of new forms in the University collections at Cambridge. *The Annals and Magazine of Natural History, 2nd Series*, **4**, 330–335.

MCILROY, D. 2004. Some ichnological concepts, methodologies, applications and frontiers, 3–27. *In* MCILROY, D. (ed.). *The application of ichnology to palaeoenvironmental and stratigraphic analysis*. Geological society, London, Special Publications, 228 pp.

MILLER, M. F. 1982. *Limulicubichnus*: a new ichnogenus of limulid resting traces. *Journal of Paleontology*, **56**, 429–433.

MINTER, N. J., BRADDY, S. J. and DAVIS, R. B. 2007*a*. Between a rock and a hard place: arthropod trackways and ichnotaxonomy. *Lethaia*, **40**, 365–375.

—— KRANIER, K., LUCAS, S. G., BRADDY, S. J. and HUNT, A. P. 2007*b*. Palaeoecology of an Early Permian playa lake trace fossil assemblage from Castle Peak, Texas, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **246**, 390–423.

OLD, R. A., SUMBLER, M. G. and AMBROSE, K. 1987. *Geology of the country around Warwick*. Memoirs of the British Geological Survey. HMSO, London.

PEMBERTON, S. G. and FREY, R. W. 1982. Trace fossil nomenclature and the *Planolites–Palaeophycus* dilemma. *Journal of Paleontology*, **56**, 843–881.

PICKERILL, R. K. 1994. Nomenclature and taxonomy of invertebrate trace fossils. 3–42. *In* DONOVAN, S. K. (ed.). *The palaeobiology of trace fossils*. John Wiley & Sons, New York, 316 pp.

POLLARD, J. E. 1985. *Isopodichnus*, related arthropod trace fossils and notostracans from Triassic fluvial sediments. *Transactions of the Royal Society of Edinburgh*, **76**, 273–285.

RADLEY, J. D. 2002. The late Triassic and early Jurassic succession at Southam Cement Works, Warwickshire. *Mercian Geologist*, **15**, 171–174.

—— 2003*a*. Warwickshire's Jurassic geology: past, present and future. *Mercian Geologist*, **15**, 209–218.

—— 2003*b*. The Triassic and Jurassic of Warwickshire: report of a 2002 Weekend Field Meeting. *Proceedings of the Geologists' Association*, **114**, 167–172.

—— 2005. Highlights of Jurassic Warwickshire. *Geology Today*, **21**, 146–152.

—— 2008. Seafloor erosion and sea-level change: Early Jurassic Blue Lias Formation of central England. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **270**, 287–294.

RADWANSKI, A. and RONIEWICZ, P. 1967. The trace fossil *Aglaspididichnus sanctacrucensis* n.gen., n.sp., a probable resting place of an aglaspid (Xiphosura). *Acta Palaeontologica Polonica*, **12**, 545–555.

ROMANO, M. and WHYTE, M. A. 1987. A limulid trace fossil from the Scarborough Formation (Jurassic) of Yorkshire; its occurrence, taxonomy and interpretation. *Proceedings of the Yorkshire Geological Society*, **46**, 85–95.

—— —— 1990. *Selenichnites*, a new name for the ichnogenus *Selenichnus* Romano & Whyte, 1987. *Proceedings of the Yorkshire Geological Society*, **48**, 221.

SAVAGE, N. M. 1971. A varvite ichnocoenosis from the Dwyka Series of Natal. *Lethaia*, **4**, 217–233.

SEILACHER, A. 1964. Sedimentological classification and nomenclature of trace fossils. *Sedimentology*, **3**, 253–256.

—— 1970. *Cruziana* stratigraphy of 'nonfossiliferous' Palaeozoic sandstones. 447–476. *In* CRIMES, T. P. and HARPER, J. C. (eds). *Trace fossils. Geological Journal Special Issue (3)*. Seel House Press, Liverpool, 547 pp.

——2007. *Trace fossil analysis*. Springer Verlag, Berlin, 226 pp.

SIMMS, M. J., CHIDLAW, N., MORTON, N. and PAGE, K. N. 2004. *British Lower Jurassic Stratigraphy, Geological Conservation Review Series, No. 30*. Joint Nature Conservation Committee, Peterborough, 458 pp.

SIMPSON, S. 1975. The morphological classification of trace fossils. 39–54. *In* FREY, R. W. (ed.). *The study of trace fossils*. Springer Verlag, New York, 562 pp.

SMITH, A. S. and RADLEY, J. D. 2007. A marine reptile fauna from the Early Jurassic Saltford Shale (Blue Lias Formation) of central England. *Proceedings of the Yorkshire Geological Society*, **56**, 253–260.

SWIFT, A. 1995. A review of the nature and outcrop of the 'White Lias' facies of the Langport Member (Penarth Group: Upper Triassic) in Britain. *Proceedings of the Geologists' Association*, **106**, 247–258.

TREWIN, N. H. 1976. *Isopodichnus* in a trace fossil assemblage from the Old Red Sandstone. *Lethaia*, **9**, 29–37.

—— 1994. A draft system for the identification and description of arthropod trackways. *Palaeontology*, **37**, 811–823.

—— and MCNAMARA, K. J. 1995. Arthropods invade the land: trace fossils and palaeoenvironments of the Tumblagooda Sandstone (?late Silurian) of Kalbarri, Western Australia. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **85**, 177–210.

VALLON, L. H. and RÖPER, M. 2006. *Tripartichnus* n. igen. – a new trace fossil from the Buntsandstein (Lower Triassic) and from the Solnhofen Lithographic Limestones, Germany. *Paläontologische Zeitschrift*, **80**, 156–166.

WALTER, H. 1983. Zur Taxonomie, Ökologie und Biostratigraphie der Ichnia limnisch-terrestrischer Arthropoden des mitteleuropäischen Jungpaläozoikums. *Freiberger Forschungshefte C*, **382**, 146–193.

WEBER, B. and BRADDY, S. J. 2004. A marginal marine ichnofauna from the Blaiklock Glacier Group (?Lower Ordovician) of the Shackleton Range, Antarctica. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **94** (for 2003), 1–20.

WISSHAK, M., VOLOHONSKY, E., SEILACHER, A. and FREIWALD, A. 2004. A trace fossil assemblage from the fluvial Old Red deposits (Wood Bay Formation; Lower to Middle Devonian) of NW-Spitsbergen, Svalbard. *Lethaia*, **37**, 149–163.

WOODS, H. 1925–31. *A monograph of the fossil Macrurous Crustacea of England*. Monographs of the Palaeontographical Society, London, 122 pp.

WOODWARD, H. 1866. On the species of the genus *Eryon*, Desm., from the Lias and Oolite of England and Bavaria (with parts of 2 plates). *Quarterly Journal of the Geological Society of London*, **22**, 494–502.

—— 1893. *The Jurassic Rocks of Britain, Vol. 3, The Lias of England and Wales (Yorkshire Excepted)*. Memoirs of the Geological Survey of the United Kingdom, London, 399 pp.

ZONNEVELD, J. P., PEMBERTON, S. G., SAUNDERS, T. D. and PICKERILL, R. K. 2002. Large robust *Cruziana* form the Middle Triassic of Northeastern British Columbia: ethologic, biostratigraphic, and palaeobiologic significance. *Palaios*, **17**, 435–448.